DOI: 10.51291/2377-7478.1754
Extending the Null Hypothesis to Invertebrate Pain Sentience
Commentary on Crump et al on Decapod Sentience

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Abstract: In 1985 Macphail proposed his Null Hypothesis that there were no qualitative differences in intelligence across vertebrate species. A recent review of the literature has found overwhelming support for his view. Studies also suggest that, with respect to cognition and the neural mechanisms that support it, the Null Hypothesis should be extended to invertebrates. We suggest, on the same premise, that the Null Hypothesis should be extended to pain sentience in invertebrates. Although few studies have been conducted, behavioural and neural evidence for pain sentience has been found in various representative invertebrate species.

Crump et al. (2022) are to be commended for developing a framework for evaluating the scientific evidence for sentience in decapod crustaceans. Most of the proposed criteria are based on aspects of pain, and of course that is critical for a determination of sentience. We approach the issue of decapod sentience from a behavioural point of view, however. We draw on similar debates in the comparative cognition literature -- about whether animals differ in intelligence and the neural mechanisms that support it -- to argue for invertebrate sentience.

In 1985 Euan Macphail proposed his famous Null Hypothesis, stating that there were no quantitative or qualitative differences in intelligence across vertebrate species. Macphail did exclude humans from his Null Hypothesis, but even the view that there were no differences in intelligence across all nonhuman vertebrate species was a dramatic statement. Macphail went on to publish his view in a 1987 target article in Behavioural and Brain Sciences, where
it received uniformly negative peer commentaries, one going so far as to say that “Macphail’s ‘null hypothesis’ is merely the epitaph on the head stone of comparative cognition” (Goldman-Rakic & Preuss, 1987, p. 667). At the time, comparative cognition was still a young science, and many of the remarkable abilities of animals that we now take for granted were unknown to Macphail. A recent re-examination of Macphail’s Null Hypothesis (Colombo, Scarf, & Zentall, 2021) resulted in overwhelming support for his view that there were no qualitative differences in intelligence among vertebrate species. Although there was agreement that there were quantitative differences across vertebrate species, the absence of qualitative differences was a clear vindication of Macphail’s view. In short, there is currently no ability present in one vertebrate species that is not also present, at least in an incipient manner, in another vertebrate species. Such a notion of quantitative differences is, of course, perfectly in line with the notion of mental continuity as advocated by Darwin (1859).

Macphail limited his Null Hypothesis to vertebrate species, in part because little was known about invertebrate cognition. The past decade, however, has seen considerable research into the cognitive abilities of invertebrates, and from our reading of the literature, we are of the view that the Null Hypothesis should be extended to include some invertebrates. For example, insects understand the concepts of same and different (Giurfa et al., 2001), can display transitivity (Tibbetts et al., 2019), and show mirror self-recognition (Cammaerts & Cammaerts, 2015), abilities that previously only fell within the domain of vertebrate species. Impressive abilities have also been seen in cephalopods (octopus, cuttlefish, and squid). For example, cephalopods (a class of mollusc) are capable of categorization (Boal, 1991), have a rudimentary sense of number (Yang & Chiao, 2016), and exhibit flexible foraging strategies and future planning abilities (Schnell et al., 2020). With respect to crustaceans in particular, Patel et al. (2021) have shown that in learning to respond to certain coloured shapes over others, mantis shrimp rely on the shape of an object rather than its colour. Although it is admittedly based on a simple task, this is a foundational ability that can support more complex forms of learning.

Despite the existence of sporadic pieces of evidence outlined in the literature (Adamo, 2016; Crook, 2021), and those outlined by Crump et al., pain sentience has generally been assumed to be absent in invertebrates. We suggest that to gain insight into decapod sentience we look at a wider range of representative invertebrate species that have been studied in greater depth at the behavioural and neural levels. Both insects and molluscs meet several of Crump et al.’s pain sentience criteria. Insects have specific nociceptors, complex flexible decision making in response to pain, and readily learn to avoid noxious stimuli (Adamo, 2016). Octopuses have been shown to have integrated nociception, with specific neural pathways that respond to pain (Crook, 2021). The octopus pain response includes wound specific grooming and successfully learning to avoid a place associated with pain. Octopuses are responsive to analgesia that prevents their pain response, and they display a preference for an analgesic condition following associative pain conditioning (Crook, 2021).

We agree with the revised behavioural criteria set out by Solms (2022), but also believe that those criteria (voluntary behaviour, learning from experiences, and working memory) are abilities shared across all vertebrates and many invertebrates. Similarly, and as raised in other commentaries, we would argue that vertebrates and many invertebrates have valenced
experiences and that they display flexible learning (Jablonka & Ginsburg, 2022). Crustaceans and insects are both arthropods and are more closely related to molluscs than to vertebrates. The combined behavioural and neural evidence from various representative invertebrates support an argument for the mental continuity of both cognitive abilities and pain sentience, both emerging prior to the divergence of vertebrates and invertebrates. We would argue that like cognitive abilities, pain sentience is a shared trait between most animals, arising in an early ancestor to vertebrates and invertebrates, rather than occurring in multiple independent evolutionary events.

For crustaceans, and other invertebrates, the threshold of evidence to ‘prove’ pain sentience, and cognitive abilities, is higher than for vertebrates. MacPhail’s Null Hypothesis aimed to discredit biases which favoured primates and mammals over other animal species in cognitive abilities. We believe the same null hypothesis should be extended to pain sentience in invertebrates.

References


